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Understanding language evolution: Beyond *Pan*-centrism

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Abstract

Language does not fossilize but this doesn't mean that language's evolutionary timeline is lost forever. Great apes provide a window back in time on our last pre-linguistic ancestor's communication and cognition. Phylogeny and cladistics implicitly conjure *Pan* (chimpanzees, bonobos) as a superior (often the only) model for language evolution compared with earlier diverging lineages, *Gorilla* and *Pongo* (orangutans). Here, in reviewing the literature, we show that *Pan* do not surpass other great apes along genetic, cognitive, ecologic or vocal traits that were putatively paramount for language onset and evolution. Instead, we revive the idea that only by abandoning single-species models and learning about the variation between great apes may we have a chance to retrieve lost fragments of the evolutionary timeline of language.

1. Introduction: Background and Objective

Three decades ago, scholars at the forefront of the study of human behavioural evolution forewarned us of the dangers and pitfalls of single-species models [1] – the practice of electing *one* particular species, often motivated by circumstantial, proximate or opportune reasons as *the* reference point for the theoretical and empirical comparative study of human evolution. In the 1950s and 60s, baboons were the prevalent model species for human behaviour evolution based on their shared (savannah) ecology and similar primate biology with early hominids [2]. This notion changed over time [3] and twenty years later, following the development of phylogenetic primate analyses in the 80s [4], the prevalent model species became chimpanzees. Primatologists at the time were, however, expeditious, quickly pointing out that living *Pan*, albeit possessing the highest phylogenetic relatedness with humans among primates, represented a "radical" and warped model for human evolution [5]. This lesson is important because living species can never be ancestral of

extinct ones [5]. Living species have undergone their own evolutionary path since an ancestral node in a way that obscures the traits that were in fact present in the ancestral node. Today, however, comparative great ape research across fields seems to have cast off these insights and remains by and large *Pan*-centric [6–9].

Fifteen million-years ago, unlike today, the world was inhabited by multiple and contemporaneous hominid species, of which at least 22 are recognized extinct genera, excluding the direct ancestors who would become genus *Homo* [10]. Given how improbable fossilization is, numbers were beyond doubt much larger than what the fossil record shows. Besides ourselves, the only surviving traces of this diversity nowadays are the seven (nonhuman) great ape species alive today, three orangutan, two gorilla, one chimpanzee and one bonobo species, comprising three genera, *Pongo*, *Gorilla* and *Pan*, respectively. Each extant great ape lineage diverged at different times from the one that eventually gave raise to *Homo* (Fig. 1). *Pongo* was the first lineage to diverge [11], *Gorilla* the second [12], *Pan* the last [13,14]. This is reflected in the level of genetic similarity between each great ape genus and humans, as well as their taxonomy. All great apes are hominids, including humans, i.e., members of the Hominidae family. Only humans and *Pan* (i.e. chimpanzees or bonobos), however, are recognised as hominins, members of the subfamily Homininae. Given this phylogenetic proximity and cladistic pedigree, an implicit principle and implication for comparative research has, thus far, been that *Pan* represents a better model for the evolutionary study of human communication and cognition [6–9].

A quick search in Google Scholar using the term "language evolution" together with the common name for each of the living great apes yields 5,620 hits for "chimpanzees", 2,090 for "bonobos", 2,200 for "gorillas" and 1,140 for "orangutans" (OR "orang-utans"). Taking these figures as a (very) rough and preliminary estimate of the current biases in great ape comparative research in the field of language evolution, ~70% of the literature focuses on *Pan* (51% chimpanzees, 19% bonobos), ~20% on *Gorilla* and 10% on *Pongo*. Pending a more systematic assessment of species' biases, our quick search helps us, at least, get a preliminary glimpse at the scale of the problem.

Our aim in this paper is to rekindle the view, and its associated cautionary tale, that single-species models are recipes for heuristic confusion and a path towards data deficit when seeking to understand human evolution and its derived traits. First, we highlight two biases that currently affect in important ways the perceived importance of *Pan*, namely with regards to its abundance and phylogeny. We argue that chimpanzee abundance has partly driven the species perceived importance and that *Pan-Homo* closeness is a poor measure of importance. We then present and evaluate four arguments that are typically used to justify the selection of *Pan* in genetics, social

cognition, ecology and vocal behaviour for the study of human behavioural evolution and more specifically, language. For each of these arguments, firstly, we show that a *Pan*-only model to human and language evolution fails to faithfully depict the putative ancestral hominid behavioural richness and variability, an image that will inherently be best inferred from analyses that span across all great ape genera. Doing so, we echo other voices [15,16] who have sought to amend some misunderstandings in human and language evolution theory and research, such as the belief that humans evolved from chimpanzees [17] and that our ancestors were chimp-like apes [18]. Secondly, we show that replacing *Pan* with any other great ape species or genus as the reference model is equally ill-advised. Acknowledging the diversity and variance of great ape traits (and more generally across animal taxa) that contributed to shape cognitive and linguistic evolution will help make new strides in the effort of reconstructing the evolutionary timeline of language.

2. Two current biases in the field

2.1. A species over-representation may distort its actual scientific importance

It is hard to design and implement animal research without assessing its practical aspects, and when it comes to species selection, availability often determines scientists' choices. Certain species are chosen not because of their importance but because they are readily available (e.g. fruit flies, mice, pigeons). However, this seemingly innocent practical consideration has created an abundance-importance loop that has created a bias in great ape research and stifled research progress. Abundance (either in the wild or captivity) translates into availability for research, which in turn translates into larger volumes of research. Larger research volume on a given species, in turn, drives the species' theoretical and empirical importance as its biology and behaviour becomes increasingly better understood. Finally, importance positively feeds back into availability and research volume, thus closing the loop. Species' importance stops being inherent to a species, but in practice a mere after-effect of its own research.

During the 19th and 20th century, this problem was aggravated as animal collections were being actively established by capturing animals from the wild. In consequence, the perceived importance of that period for a certain species also drove its capture in the wild, increasing consequently availability (and thus, research output), ultimately self-fulfilling the premise of the species' importance. An example is the case of the capture of 130 hamadryas baboons, housed during the 1930s at the London Zoo, which caused a flood of studies that eventually became influential in fuelling the baboon-based single-species model of the 60s [2]. Given serious ethical and conservation concerns nowadays [19], wild capture by accredited zoological institutions is now a virtually extinct practice. This has disrupted the chicken-and-egg issue of abundance driving

importance driving abundance. However, it has also generated a limitation that modern scientists must work with, particularly in captivity. The existing zoological collections are a legacy of the scientific values (and perceived importance) of the 19th and 20th century that have been passed on to modern primatology, evolutionary anthropology and comparative psychology. They do not reflect current values or knowledge. Abundance in the wild has also shaped research and species importance in similar, though less circular, ways.

Today, chimpanzees show the highest abundance among all great apes. In captivity, they comprise the largest collections, and in the wild their wide-spread range covers virtually the full length of the African East-West continental axis. One could perhaps justify the current abundance-importance match for chimpanzees by invoking their phylogenetic closeness to humans (see below). They are, after all, our closest living primate relatives. Should we therefore be so concerned about the criteria that define a species importance? Though abundance can justify importance, it is not a criterion for it. Otherwise, bonobos – chimpanzees' sister species – would be equally represented in the literature, yet, they remain largely understudied. There have been clear efforts to correct this discrepancy in research effort within *Pan* [9]. Some of these attempts have, however, "simply" removed chimpanzees and set bonobos in their place within the *Pan*-centric framework, preserving indirectly a single-species approach for the study of human behavioural evolution. Neither option is suitable because an excessive reliance on phylogenetic closeness to humans can still be problematic, as we discuss next.

2.2. Phylogeny is a misleading indicator of a species scientific importance

The fact that the surviving hominid lineages today are *Homo*, *Pan*, *Gorilla* and *Pongo* is a historic artefact. Some say an accident [20]. If we played the tape of life again (paraphrasing S.J. Gould), other fossils would likely be known, other lineages would be likely alive and/or the same lineages would likely show a suite of different traits, as slight differences would have compounded differently over evolutionary time (Fig. 1).

It is important, therefore, to bear in mind that *Pan* and *Homo* have been assigned a separate taxon (Homininae) because *Pan* happens to be our closest-related hominids alive today. If hypothetically speaking, some ape lineage that had diverged more recently from the human lineage than *Pan* were still alive (Fig. 1), it would probably be classified as Homininae and, furthermore, it would displace chimpanzees and bonobos from it. We believe that, even if chimpanzees and bonobos turned out not being our closest living relatives, their dismissal as useful models of human and language evolution would be unjustified. In another possible evolutionary scenario, if *Pan* had become extinct in a distant past, one would be justified to choose *Gorilla* as the new model for

human and language evolution (Fig. 1). However, given the various differences between *Gorilla* and *Pan*, this would result in very different hypotheses for human and language evolution. Even within our current evolutionary universe (i.e. *Homo*, *Pan*, *Gorilla* and *Pongo*) (Fig. 1), some researchers have described how present day great ape distribution in the wild, and a fragmentary fossil record, can contribute to the misrepresentation of the natural history of these lineages, their origins, dispersions and relationships within Eurasia over the last 10 to 15 mya [21].

These and other limitations that come to light through our knowledge of the workings of evolution must be recognized. The consequence is that one cannot easily justify electing *Pan* as a privileged model to gain insight into human evolution in detriment of other living great apes. *Pan* is a privileged comparative model and so are the other last surviving great apes. While work on *Pan* is valuable, it is time we embrace the full diversity across great apes (and beyond) to draw as much information as possible to re-build the lost continuity between ourselves and our last pre-linguistic ancestor.

In the next section, we address the main arguments typically used to justify *Pan*'s importance and closeness for the study of human cognitive and behavioural evolution. We don't dismiss the importance of these arguments unreservedly but evaluate each of them critically as criteria for the choice of a model species in the study of language evolution. We start with genetics, the golden standard for gauging phylogenetic closeness to humans among great apes.

3. Why *Pan*-favouritism is unwarranted in the study of language evolution

3.1. Genetic similarity does not automatically translate into similarity of language-like traits

Members of *Pan* represent the last extant lineage to have diverged from the human clade. Hence, they exhibit the highest levels of genetic similarity with humans among all great apes and this has been a primary motivator for a *Pan*-centric approach to language evolution. Although *Pan-Homo* genetic relatedness in comparison to *Gorilla-Homo* or *Pongo-Homo* is undisputable, it is also misleading. Notably, because it is a measure of *overall* genetic similitude. It is not a measure of the genetic similitude between genome sections that have known implications for the development of behavioural and/or cognitive mechanisms, including those underpinning language. Analyses of hominid genome regions known to encode structures and functions involved in communicative behaviour and cognition, such as the FOXP2 great ape orthologs, for example [22], render a much subtler picture than that sketched by overall genetic relatedness or bare cladistics. Humans with altered versions of the FOXP2 gene show, besides severe speech and language impartment, changes in the structure and activation of the cortex, basal ganglia and cerebellum [23]. Expression of the gene is also involved in heart and lung tissues, for example, but its role is specifically

associated with the neurological development of circuitry responsible for motor coordination and vocal production [23].

Humans have a unique FOXP2 structure, which differs from that of chimpanzees, gorillas and rhesus macaques, namely, two nonsynonymous amino-acid substitutions have been fixed in the human version of the gene. Because there have been no fixed substitutions between chimpanzees, gorillas and rhesus macaques, their gene structure represents the putative primate ancestral state. There is, however, a catch. Orangutans have accumulated a unique fixed nonsynonymous amino-acid substitution [24]. This substitution is not similar to any of the two human substitutions. This mismatch may perhaps justify its dismissal but a deeper look reveals otherwise. Mutated versions of the human gene with only one substitution (instead of two) cause grave speech and language impairments, demonstrating that the evolution of the gene in the human clade was not simply a two-step up from its primate ancestral form. This means instead that intermediate stages in gene structure likely involved *one* or more substitutions *at different loci* in the gene until the present human structure came about. The existence of an orangutan substitution at a different locus seems, thus, to be evolutionarily more pertinent than, thus far, recognized. Indeed, whilst described in the original paper [24], subsequent reviews on the matter seem to omit any mention of it and fail to consider altogether the true implications of orangutan's version of the gene [23].

Indeed, recent detailed analyses have confirmed that this unique amino-acid substitution in *Pongo* encompasses structural and functional changes in the orangutan biochemical phenotype [22]. This demonstrates that this substitution has structural consequences in individuals' phenotype and that their biological makeup would be different without this substitution in terms of the circuitry involved in motor skills and vocal articulation and control. While the strand of research on great ape FOXP2 orthologs is still in its infancy, these phenotypical effects seems to be potentially linked and help explain some of the remarkable language-like and sophisticated vocal learning and vocal invention capacities described in *Pongo* [25–28]. If measured by the number of FOXP2 amino-acid substitutions since the last great ape common ancestor, only orangutans and humans have accumulated functional substitutions.

One could feel perhaps tempted to turn to *Pongo* as the new single-species model for language evolution. However, other types of genetic alterations within FOXP2 that occur across *all* great apes indicate that any single-species model is unsuitable. For example, it is now established that microsatellite variation and nonsynonymous polymorphisms occur across orangutans, gorillas and chimpanzees in non-negligible frequencies [22]. Such variation only partially overlaps between great apes and could tie back to cases of voluntary breathing control [29] and variation in vocal

repertoire composition in gorillas [30] or described events of vocal learning [31–36], intentional vocal signalling [37–41] and concurrent activations and architectural changes in Broca's homolog brain region in chimpanzees [42–44]. Choosing *Pan, Gorilla* or *Pongo* as a basis for a single-species model would deprive the theory of human and language evolution of relevant information: namely the contribution that each great ape species can make to the larger picture, made up of different, but interlocking pieces of data.

3.2. No great ape is cognitively "greater" than the other

Language is fundamentally a cultural system that requires specific cognitive processes to be in place. Does *Pan* cognition show considerable differences with regard to the other great apes that could bear on the evolution of language-like cultural systems? The answer seems to be negative. All great ape species exhibit cognitive mechanisms of social learning and transmission that allow for the emergence of new innovations and their diffusion through populations, which subsequently become local traditions [30,45,46]. The gamut of traditions exhibited by any particular population varies across great ape genera, defining each population's specific and unique cultural repertoire [45].

In captivity, where socio-ecological conditions are often virtually equal across great ape genera, *Pan* does not consistently outperform other great ape genera in social cognition measured either as single tasks [47–49], or as part of a multi-item test battery [50]. Even after including tasks measuring non-social domains, many studies still show no clear-cut differences between genera [51–55], and when differences exist [50,56,57], it is not always the case that *Pan* consistently outperforms the other great ape genera. For instance, chimpanzees outperform orangutans in object permanence and causality tasks [50] but the reverse seems to be true in some problem-solving tasks [56–58]. There is, therefore, no compelling evidence that any of the great ape species consistently outclasses all the others in every domain. In fact, one of the few results that does seem consistent and generalizable across studies is that individual variation within species is vast and in some cases as large between individuals of the same species as individuals of different species. At the same time, different great ape species can be more similar to each other in captivity than captive and wild counterparts of the same species (for example, with regard to terrestriality and tool use, [59]).

3.3. Lessons learned about the ecology of language evolution from each great ape species

Hominid evolution was affected by the uplift of the East African Plateau [60], which disrupted climatic cycles and caused pulse events of high climate variability and long-term increase of dry and arid ecosystems [61]. These processes have presumably driven hominid diversification,

including speciation events along the human clade, and thus, to have driven directly or indirectly the emergence of language. It could be argued that within *Pan*, savannah chimpanzees provide unique models since they live today in some of the most arid habitats inhabited by any living great ape [62–64]. While true and revealing, a *Pan*-centric approach to language evolution based on ecology will nonetheless defect in how much information it can generate about the ecology of human and language evolution. For example, Bornean orangutans (*P. pygmaeus*), while inhabiting rain forests, experience some of the most extreme events of food variability between mast years, so much so that they enter in ketosis and endure periods of negative protein balance during the most severe and meagre seasons [65]. Differences in habitat between eastern and western Gorillas (*G. beringei* and *G. gorilla*), covering some of the highest ranges of elevations and altitudes within any great ape genus, can potentially provide likewise a uniquely informative scenario for divergence events of hominid biology and communication driven by climate, particularly in light of the far-reaching continent-wide range of human ancestors and archaic humans [66]. The same applies for Bornean orangutans experiencing food scarcity and their counterparts inhabiting the fertile peat-swamps of the West coast of Sumatra [67], or between savannah and forest-dwelling chimpanzees.

Besides providing the physical stage for communication, habitat type is also a direct determinant of a species' diet. Indeed, new evidence from phylogenetic analyses [68] and mathematical modelling [69] indicates that ecological (other than social) challenges were a primary driver for brain expansion within the human clade. Understanding the direct (e.g. habitat acoustics) and indirect (e.g. productivity, diet, energetics) ecological challenges that the hominid family experienced during and after the Miocene, including the direct ancestors of *Homo*, and the adaptation of their communication and signal systems, will advance faster if we begin to draw comparisons *within and between* extant great ape genera.

3.4. Living links between great ape vocal skills and human verbal skills

Speech is the only universal medium of language. That is, each and every human population exhibits, at least, one spoken language. Spoken language is also the basis for virtually all major writing systems, wherein symbols encode sound (typically of phonemes or syllables). For these reasons, the vocal capacities of great apes have historically been a key component in the study of possible precursors and processes for language evolution within the human clade [70–72]. Originally, during the 1960s, one of the predominant hypotheses was that speech, as the primary means expression of language, was hampered in nonhuman species due to anatomical constraints that imposed crucial limitations for speech production [73,74]. Today, however, various strands of data suggest that, even though the evolution of speech has left a mark in human anatomy [75], primate

vocal anatomy does not represent a serious impairment for speech-like production. Different anatomies would have generated slightly different vocal output but speech-like expression would have been possible nevertheless [76–80]. These data compelled some scholars decades later to assume that great apes could not speak because they "didn't have the brains", or in other words, that neural anatomy (instead of vocal anatomy) prevented speech production (reviewed in [27]). A renewed interest in great ape vocal capacities over the last few years is generating a growing body of evidence that is disproving this idea [27]. New evidence includes and is not limited to, for example, the capacity for vocal invention [81], vocal learning [32,33,82], production of consonant- and vowel-like calls [28,83,84], learned vocal production at speech-like rhythm [80], complex (non-Markovian) vocal sequences [85], call traditions and cultures [30,86,87], vocal tools and manipulations for the generation of rare acoustic phenomena [88,89], intentional vocalizations [37,39,40], deceptive vocal responses [88], and time-space vocal displacement [26]. Findings for advanced vocal skills in great apes are supported by convergent inter-disciplinary lines of evidence, from great ape genomics [22,90] to great ape neurology and neurophysiology [91], indicating that "[t]he inter-mediate vocal phenotype of non-human great apes [between Old-World monkeys and humans] suggests that selection for increased vocal-motor control had already begun at the time of the last common ancestor of the great ape lineage" [91].

Moreover, recent research shows that within *Pan*, chimpanzees and bonobos have experienced arguably some of the most accelerated divergence in vocal anatomy among great apes, even though they represent sister species [92,93]. This shows that opting for a *Pan*-centric approach ignores the rich and informative differences both within that genus and the evolutionary paths taken by each great ape species, each unique and potentially revealing in its own way. Findings regarding gestural communication in great apes, including inter-species comparisons, evoke a similar general interpretation [94–96].

Altogether, the burgeoning strand of great ape vocal research [27,91,97] shows that traditional ideas about what great apes can and (mostly) cannot do are outdated, too crude or unsubstantiated. The precursor system for (spoken) language evolution will be best understood when zooming out our theoretical and empirical lenses to include the vocal (and gestural) behaviour of all great ape genera, including its neural and molecular substrates.

4. Concluding remarks and future perspectives

Notwithstanding the closer overall genetic and taxonomic proximity of *Pan* with humans, comparative research across great apes in the fields of genetics, cognition, ecology, and vocal

behaviour does not elect *Pan* as being a more preferred or better suited model for the study of language evolution. This ought also to apply to the evolutionary study of other aspects of human cognition and communication. As explored and reviewed here across fields, single-species models will inevitably result in fragmentary data and piecemeal accounts of the evolutionary history of language or any of its particular traits, whatever the chosen model species may be. Therefore, our intention here is not to transform a (*Pan*-centric) single-species paradigm into another single species, genus or family-based paradigm. Much remains to be learned from an ever-wider taxonomic approach to language evolution. Data from many species can contribute to our understanding of this unrepeated phenomenon that has only occurred in our lineage during the period of about 3.5 billion years of life on Earth.

Language evolution is perhaps one of the most fabulous puzzles to have tantalized philosophers, scholars, naturalists, and scientists throughout the centuries. To stand a chance of understanding its evolution, we need to consider non-exclusively all the lines of evidence potentially available – lines that ought to extent as far down in the tree of life (thus, include as many species) as possible. Fully acknowledging the diversity in great ape cognition and communication is an important and necessary step in this direction. As our closest relatives, they complement in a unique way what can only be gleaned from the fossil record. Great apes represent an empirical gem of sorts and we must cherish their present, importance and current diversity, before it is too late [19,98]. Each and every great ape, individual and species, will provide unique lost fragments about our own past and history, including about the timeline of the feature that best characterises us – language.

Conflicts of Interest

The authors declare that they have no competing interests.

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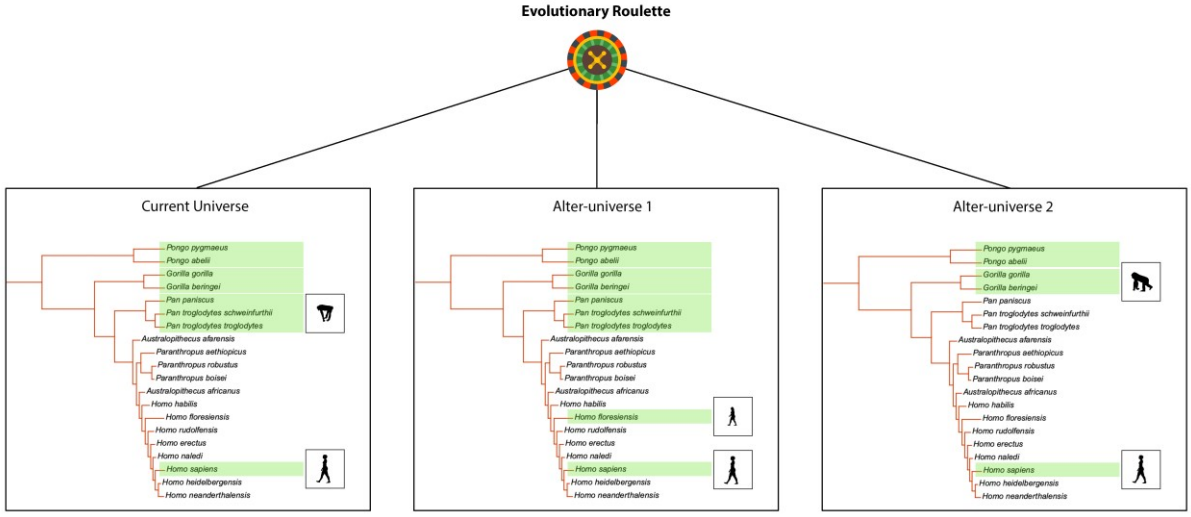

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336 **Legends**

337 Figure 1. The great evolutionary roulette and our understanding of human evolution. The
338 evolutionary roulette has innumerable possible outcomes, one of which is our current universe
339 (green shades indicate extant lineages), where the closest living relatives to humans (within black
340 squares) today are member of *Pan*. Different evolutionary outcomes would generate, however,
341 alter-universes (1 and 2) where other lineages closer related to humans would be alive or extinct
342 today. Phylogenetic tree replicated from [99] under Creative Commons license.

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